TEMPORAL PATTERNS IN THE DIET AND FOOD PARTITIONING IN IMPERIAL CORMORANTS (*PHALACROCORAX ATRICEPS*) AND ROCK SHAGS (*P. MAGELLANICUS*) BREEDING AT BAHÍA BUSTAMANTE, ARGENTINA

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ABSTRACT.—We studied the diet of Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*P. magellanicus*) at Bahía Bustamante, Argentina, between 1992 and 1994. We analyzed pellet casts (1887 from Imperial Cormorants and 799 from Rock Shags) and regurgitations of stomach contents (260 from Imperial Cormorants and 24 from Rock Shags). Imperial Cormorants and Rock Shags fed on at least 22 and 21 different types of prey, respectively. The main prey species during all study years were fish: *Engraulis anchoita* for Imperial Cormorants and *Patagonothen* sp. for Rock Shags. For both species, the consumption of the main food categories as estimated by pellet analysis was similar among years. A significant relationship was found between Imperial Cormorant and Rock Shag diets during the three years, while the diet overlap index was relatively high. During all years, Imperial Cormorants consumed a significantly larger proportion of pelagic or demersal fish than did Rock Shags, while Rock Shags consumed benthic fish in a greater proportion than did Imperial Cormorants. Mean maximum diving depth, determined using capillary tube depth gauges, of Imperial Cormorants (24.4 m ± 18.8 SD) was significantly greater but more variable than that of Rock Shags (9.3 m ± 4.1 SD). *Received 29 October 2002, accepted 10 March 2003.*

Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*Phalacrocorax magellanicus*) are widely distributed along the Argentine coast (Yorio et al. 1998). The Imperial Cormorant is a relatively abundant seabird, with nearly 50,000 breeding pairs in colonies of up to several thousand nests, whereas the Rock Shag has a population of >7,000 pairs distributed in relatively small colonies (Yorio et al. 1999). Despite the wide distribution of these cormorant and shag populations, relatively little is known about their diet and food partitioning. Few studies on their diets have been conducted along the Patagonian coast, and these have focused on only a single species and breeding season (Malacalza et al. 1994, 1997; Gosztonyi and Kuba 1998) or have been based on a small sample size (Punta et al. 1993). Foraging patterns and diving behavior have been reported at only two Patagonian sites (Quintana 1999, 2001; Sapoznikow and Quintana 2003). At most breeding locations in Patagonia, these two species share

the same colony sites (Punta 1989, Gandini and Frere 1998, Schiavini et al. 1998). However, no studies yet have quantitatively analyzed food partitioning between these congeneric cormorant species. The objectives of this study were to (1) analyze the diet and maximum diving depths of breeding Imperial Cormorants and Rock Shags during three years at Bahía Bustamante, Golfo San Jorge, (2) compare the results with those previously obtained at other Patagonian locations, (3) analyze diet variation among years and stages of the breeding cycle, and (4) assess food partitioning between the two species.

METHODS

Diet sampling and analysis.—We studied the diets and diving behavior of Imperial Cormorants and Rock Shags in the Bahía Bustamante area (45° 05′ S, 66° 28′ W to 45° 13′ S, 66° 30′ W), Golfo San Jorge, Chubut, Argentina. We collected pellets in active nests (1,887 samples from Imperial Cormorants and 799 from Rock Shags) and obtained regurgitated stomach contents from birds when we approached their nests (260 samples from Imperial Cormorants and 24 from Rock Shags). Samples were gathered mostly at colonies of both species at Isla Galiano. In addition, we obtained diet samples at other breeding sites, including Islas Lobos, Isla Ezquerra, Isla Ver-

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naci Este, Isla Vernaci Oeste, and Isla Viana, all 6.5–11 km from Isla Galiano.

We collected samples from early November to February in 1992 and from October to February in both 1993 and 1994. We visited colonies at 1- to 4-week intervals during 1992 and 1994, and at 1- to 2-week intervals during 1993. During each visit we noted the breeding status of nests within the study areas. We froze regurgitates and dried pellets until we examined them in the laboratory. We examined each sample with a microscope (21× magnification) and identified food remains to the lowest taxonomic level possible, using fish otoliths, squid beaks, crustacean shell fragments and chelae, mollusks shell fragments, polychaete mandibles and chetae, and echiurid remains. We identified prey with the aid of published guides (Torno 1976, Menni et al. 1984, Clarke 1986, Boschi et al. 1992) and a reference collection obtained from the study area.

For each prey species, we recorded the percentage of occurrence from pellets and percent mass from regurgitates. For the analysis of seasonal variation in diet we used only pellet samples, and grouped prey into five prey categories (fish, crustacean, cephalopod, echiurid, and polychaete). We divided the breeding cycle into four stages: prelaying, incubation, young chicks (chicks up to the first molt, approximately 4 weeks of age), and old chicks (chicks between the first molt and fledging).

Diving behavior.—We studied maximum diving depth of Imperial Cormorants and Rock Shags with capillary tube depth gauges during 1994. We attached depth gauges (Burger and Wilson 1988) on 162 Imperial Cormorants and 90 Rock Shags. The gauges were taped to wing feathers and we retrieved them mostly (71.6%) within 24 h of deployment (83.2% within 48 h). After recovering a gauge, we measured to the nearest 0.05 mm the length of the tube still covered with indicator powder; gauges that were difficult to read were eliminated from the analysis. We calculated maximum depth with the equation: $D_{max} = 10.08 (L_i/L_d - 1)$, where D_{max} is the maximum depth attained (in m), L_i is the initial length of undissolved indicator powder (in mm), and L_d the length on recovery (in mm) (Burger and Wilson 1988).

Statistical analysis.—We used G-tests to an-

alyze the variation of each food category throughout the breeding cycle and to conduct comparisons among locations and between years. We used ANOVAs to analyze differences in consumption among prey categories and the number of prey taxa per pellet among stages of the breeding cycle. To compare diets of Imperial Cormorants and Rock Shags, we used a Spearman correlation coefficient, ranking prey according to their frequency of occurrence (Ashmole and Ashmole 1967). We evaluated diet overlap between both species using the Morisita index. We used nonparametric tests whenever underlying assumptions were not met.

RESULTS

Imperial Cormorant diet.—Pellet analysis indicated that Imperial Cormorants fed on a wide variety of prey during all years, including at least 22 different types of prey (Table 1). Fish were the most frequently identified prey during the three years, followed by crustaceans and cephalopods. We identified 20 prey types from regurgitate samples, including the crustacean *Peisos petrunkevitchi*, which was not detected in pellets. The main prey species during all study years was the fish *Engraulis anchoita*. Fish consumption, measured as mean wet mass, during the three years was significantly greater than that of crustaceans, cephalopods, echiurids, and polychaetes (ANOVA $F_{5,423} = 16.2$, $P = 0.0001$). The percentage of fish by wet mass was over 70% in all years (Table 1).

Consumption of food categories as estimated by pellet analysis was similar among years ($G_4 = 3.49$, $P = 0.48$). During 1993, consumption of fish as estimated by pellet analysis was similar among all stages of the breeding cycle ($G_3 = 6.16$, $P = 0.10$), while the consumption of prey from the rest of the food categories throughout the season was highly variable (all $G_3 > 9.0$, all $P < 0.05$; Fig. 1). During 1994, consumption of fish, mollusks, and crustaceans was similar among breeding stages (fish: $G_3 = 2.60$, $P = 0.46$; mollusks: $G_3 = 1.10$, $P = 0.78$; crustaceans: $G_3 = 4.47$, $P = 0.21$), while the proportion of polychaetes and echiurids in the diet varied throughout the season (polychaetes: $G_3 = 13.32$, $P = 0.004$; echiurids: $G_3 = 11.07$, $P = 0.011$; Fig. 1). The number of prey taxa per pellet increased dur-

TABLE 1. Prey consumed by Imperial Cormorants at Bahía Bustamante, Argentina, 1992–1994, obtained by pellet and regurgitate analysis. Sample size is in parentheses.

Taxa	Percentage occurrence in pellets			Percent fresh mass in regurgitates		
	1992 (1,350)	1993 (275)	1994 (262)	1992 (95)	1993 (115)	1994 (50)
Fish	93.3	96.0	96.6	72.3	71.8	79.0
Engraulis anchoita	58.4	42.5	54.2	56.3	28.1	30.8
Patagonothen sp.	43.2	41.5	45.4	6.7	9.2	13.5
Ribeiroclinus eigenmanni	45.3	28.4	31.3	1.8	9.3	1.7
Raneya brasiliensis	5.2	33.5	52.7	—	3.9	12.5
Agonopsis chiloensis	3.9	20.0	24.8	0.3	0.2	0.4
Odontesthes smitti	12.2	45.8	46.6	—	3.9	1.0
Odontesthes incisa	11.9	14.6	17.9	—	0.3	—
Merluccius hubbsi	4.6	37.1	43.9	0.8	11.9	10.1
Eleginops maclovinus	0.7	12.4	17.9	—	—	—
Ramnogaster arcuata	1.7	9.1	14.1	1.7	—	5.0
Percophis brasiliensis	1.3	1.1	5.0	—	—	—
Genypterus blacodes	1.5	7.6	24.4	1.5	4.3	—
Stromateus brasiliensis	0.4	—	—	—	—	—
Unidentified fish	0.9	0.4	—	3.2	0.7	4.0
Crustaceans	69.8	55.1	69.8	8.2	12.5	10.8
Betaeus truncatus	58.8	34.5	49.6	1.4	4.4	4.9
Peltarion spinosulum	17.9	17.1	16.0	0.7	5.9	3.4
Pleoticus muelleri	1.2	3.3	8.4	0.7	0.3	—
Munida subrugosa	2.7	12.0	14.5	4.5	1.4	1.2
Lithodes santolla	—	5.8	9.2	—	—	1.3
Peisos petrunkevitchi	—	—	—	0.9	0.5	—
Cephalopods	57.5	60.9	61.8	6.5	7.0	6.5
Octopus sp.	47.4	33.5	35.5	5.2	5.9	3.5
Loligo gahi	16.3	38.2	40.8	1.3	1.1	3.0
Echiurids	44.2	35.6	39.7	4.0	3.3	1.5
Polychaetes	74.2	41.1	48.5	2.6	2.6	1.8
Aphrodita sp.				—	—	—
Polinoe sp.				—	—	—
Unidentified prey	2.7	0.4	1.1	6.4	2.8	0.4
Total mass (g)				3,722.1	7,143.8	4,806.5

ing the breeding season, reaching maximum values during the early chick stage (1993: ANOVA $F_{3,270}$ = 14.5, P < 0.0001; 1994: ANOVA $F_{3,252}$ = 7.2, P = 0.0001; Table 2).

Rock Shag diet.—Pellet analysis indicated that Rock Shags fed on a wide variety of prey during all years, including at least 21 different types of prey; fish were the most frequently identified prey during the three years, followed by polychaetes and crustaceans (Table 3). The main prey species were *Patagonothen* sp. and *Ribeiroclinus eigenmanni*. We identified 20 prey types from the regurgitates. Fish consumption, measured as mean wet mass during both 1993 and 1994, was significantly greater than that of crustaceans, cephalopods, echiurids, and polychaetes (ANOVA $F_{4,64}$ = 2.7, P = 0.039). The percentage of fish wet

mass was over 90% in 1994, but was only about 40% in 1993 (Table 3). Regurgitate analysis indicated that *Patagonothen* sp. was the main prey species in both years (Table 3).

The consumption of the food categories as estimated by pellet analysis was similar among years (G_4 = 1.55, P = 0.82). During 1993, the consumption of fish, mollusks, and echiurids varied significantly among stages of the breeding cycle (fish: G_3 = 9.34, P = 0.025; mollusks: G_3 = 11.74, P = 0.008; echiurids: G_3 = 8.50, P = 0.037), while the consumption of crustaceans and polychaetes was similar (crustaceans: G_3 = 6.67, P = 0.083; polychaetes: G_3 = 0.29, P = 0.96; Fig. 2). During 1994, the consumption of echiurids throughout the season was highly variable (G_3 = 11.49, P = 0.009), while no significant sea-

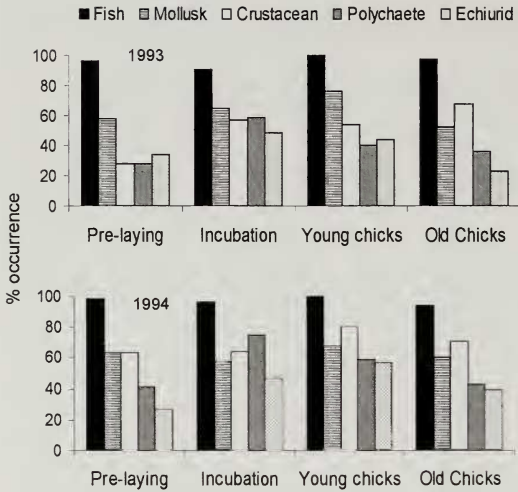■ Fish ▨ Mollusk □ Crustacean ■ Polychaete □ Echiurid

FIG. 1.   Seasonal variation in the main prey types of Imperial Cormorants at Bahía Bustamante, Argentina, during 1993 and 1994.

sonal variation was detected for the other food categories (all $G_3 < 7.69$, all $P > 0.05$; Fig. 2). During 1993 and 1994, the number of prey taxa per pellet increased with the breeding season, reaching maximum values during the late chick stage (1993: ANOVA $F_{3,236} = 9.0$, $P < 0.0001$; 1994: ANOVA $F_{3,188} = 4.2$, P < 0.007; Table 2).

Comparison between Imperial Cormorant and Rock Shag diet.—Imperial Cormorants and Rock Shags shared most of the prey types. All prey types identified in Rock Shag samples also were consumed by Imperial Cormorants. A significant correlation was found between their diets during all three years

(1992: $r_s = 0.86$, df = 19, $P = 0.0001$; 1993: $r_s = 0.73$, df = 19, $P = 0.001$; 1994: $r_s = 0.70$, df = 19, $P = 0.002$), and the diet overlap index was relatively high (1993: C = 0.67 and 1994: C = 0.69).

During 1993 and 1994, Imperial Cormorants consumed a significantly larger proportion of pelagic or demersal fishes than did Rock Shags (1993: $\chi^2 = 10.5$, df = 1, $P = 0.001$; 1994: $\chi^2 = 20.1$, df = 1, $P < 0.0001$), while Rock Shags consumed benthic fishes in a greater proportion than did Imperial Cormorants (1993: $\chi^2 = 36.2$, df = 1, $P < 0.0001$; 1994: $\chi^2 = 9.8$, df = 1, $P = 0.002$; Table 4).

Diving behavior.—A total of 41% and 31% of depth gauges deployed on Imperial Cormorant and Rock Shags, respectively, were recovered. Mean maximum depth of Imperial Cormorant (24.4 m ± 18.8 SD, range = 5.7–78.1 m, $n = 67$) was significantly greater than that of Rock Shags (9.3 m ± 4.1 SD, range = 3.8–21.0 m, $n = 28$; Mann-Whitney Z = 5.5, $P < 0.0001$; Fig. 3). Maximum depths attained by Imperial Cormorants were more variable than those of Rock Shags (CV: 0.77 versus 0.44, respectively).

DISCUSSION

Diet analyses showed that fish were the main prey consumed by both Imperial Cormorants and Rock Shags at Bahía Bustamante. Our results agree with those obtained for both species at other locations along the northern Patagonian coast. Malacalza et al. (1994) and Gosztonyi and Kuba (1998) reported that Imperial Cormorants at Punta León and Punta

TABLE 2.   Number of prey taxa per pellet (mean ± SD) of Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994 during the four stages of the breeding cycle. Sample size is in parentheses.

Year and species	Pre-laying	Incubation	Young chicks	Old chicks
1993				
Imperial Cormorant	3.4 ± 1.7 (50)	5.3 ± 2.5 (74)	6.2 ± 2.0 (50)	5.4 ± 2.7 (100)
Rock Shag	4.7 ± 2.2 (80)	5.4 ± 1.9 (35)	6.3 ± 2.2 (85)	6.8 ± 2.5 (40)
1994				
Imperial Cormorant	5.7 ± 2.7 (68)	6.3 ± 2.9 (28)	8.2 ± 2.7 (46)	6.2 ± 3.3 (120)
Rock Shag	5.5 ± 2.0 (70)	5.3 ± 2.0 (19)	5.2 ± 2.2 (28)	6.7 ± 2.9 (75)

TABLE 3. Prey consumed by Rock Shags at Bahía Bustamante, Argentina, 1992–1994, obtained by pellet analysis and regurgitate analysis. Sample size is in parentheses.

Prey	Percentage occurrence in pellets			Percent fresh mass in regurgitates	
	1992 (367)	1993 (240)	1994 (192)	1993 (10)	1994 (12)
Fish	91.9	89.6	93.2	41.4	93.8
Engraulis anchoita	47.0	33.3	38.0	—	16.3
Patagonothen sp.	67.4	69.6	75.0	33.1	43.1
Ribeiroclinus eigenmanni	68.8	62.1	67.7	8.3	9.5
Raneya brasiliensis	1.9	12.5	15.6	—	9.2
Agonopsis chiloensis	11.1	42.1	52.6	—	—
Odontesthes smitti	3.3	35.0	29.7	—	2.4
Odontesthes incisa	7.9	13.3	13.5	—	—
Merluccius hubbsi	1.9	9.6	10.9	—	—
Eleginops maclovinus	2.2	19.2	14.1	—	—
Ramnogaster arcuata	0.8	8.3	7.3	—	—
Percophis brasiliensis	1.4	5.8	3.1	—	—
Genypterus blacodes	0.0	1.3	2.6	—	2.1
Unidentified fish	1.4	—	—	—	11.2
Crustaceans	70.6	64.2	67.7	21.0	6.2
Austropandalus grayi				—	—
Betaeus truncatus	58.2	59.2	65.1	8.1	3.4
Nauticaris magellanica				—	—
Campylonotus vagans				—	—
Peltarion spinosulum	16.9	14.2	16.2	11.4	2.8
Leucippa pentagona				—	—
Pleoticus muelleri	3.3	—	—	—	—
Munida subrugosa	3.0	6.3	3.1	1.5	—
Lithodes santolla	—	—	0.5	—	—
Cephalopods	60.3	55.8	59.9	15.5	—
Octopus sp.	56.3	45.0	50.0		
Loligo gahi	9.5	17.1	17.2	—	—
Echiurids	60.1	39.2	34.4	7.1	—
Polychaetes	84.0	75.4	71.4	15.0	—
Aphrodita sp.				—	—
Polinoe sp.				—	—
Unidentified prey	3.3	0.4	2.1	—	—
Total mass (g)				574.7	524.3

Lobería had similar diets, with fish being the dominant prey. Fish also was the main prey type reported for other species of the "blue-eyed cormorant complex" breeding in other regions (Brothers 1985, Espitalier-Noel et al. 1988, Green et al. 1990, Wanless et al. 1992, Ridoux 1994, Casaux et al. 1997, Favero et al. 1998). Relatively fewer references are available on Rock Shag diet throughout its range, and these show that fish also are their main prey (Bahamonde 1955, Punta et al. 1993, Malacalza et al. 1997).

Previous studies have shown that Imperial Cormorants include a variety of fish species in their diet. At Punta León, diet included seven species, mainly *Triathalassothia argentina* and *Raneya fluminensis*, of which four are common to our study (Malacalza et al. 1994). At Punta Lobería, Gosztonyi and Kuba (1998) found a total of 12 fish species, mostly *Tripterygion cunninghami*, *Engraulis anchoita* and *Patagonothen* sp. Our results in Bahía Bustamante showed a similar number of species, although only half of them are shared by both cormorant populations. Differences also were found in a previous study conducted at Bahía Bustamante based on a relatively small sample size, where a lower number of fish species was reported (Punta et al. 1993). Given the small interannual variability observed in this study, differences observed are likely due to differences in the analytical methods applied in the two studies. During all three years of the present study, crustaceans, ceph-
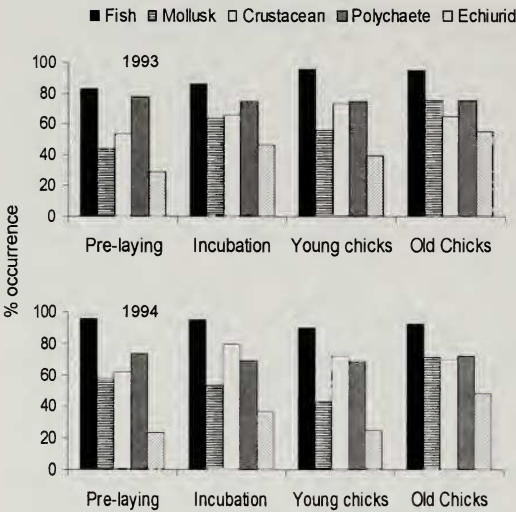
FIG. 2.   Seasonal variation in the main prey types of Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994.

FIG. 3.   Frequency distribution of maximum diving depths for Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1994.

alopods, echiurids, and polychaetes comprised the diet of Imperial Cormorants and Rock Shags. However, the proportion of polychaetes in pellet samples of both species may have been overestimated, polychaetes being the result of secondary consumption (Casaux et al. 1995, Johnson et al. 1997).

At Bahía Bustamante, Imperial Cormorants and Rock Shags preyed upon a wide variety of fish and invertebrates found in different coastal habitats, including benthic, demersal, and pelagic areas. Benthic prey included fish found on rocky, sandy, and muddy bottoms. Fish, such as *Patagonothen* sp., *Agonopsis chiloensis* and *Ribeiroclinus eigenmanni*, live in inshore habitats among algae (Gosztonyi and Kuba 1998). Such flexibility in feeding
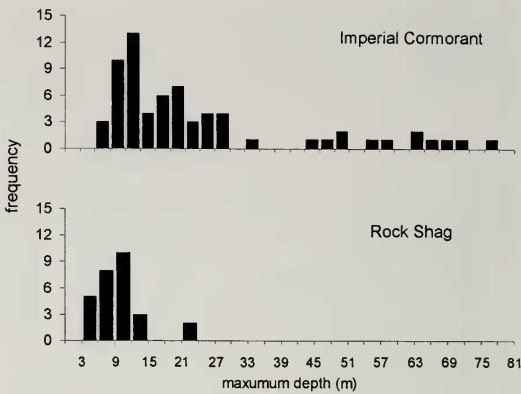
habits also has been reported for other cormorants, and it was argued that this flexibility plays an important role in maximizing cormorant food intake (Grémillet et al. 1998).

Punta et al. (1993) reported changes throughout the breeding cycle in the diet composition of Imperial Cormorants, with an increase in the consumption of fish, particularly *Engraulis anchoita* and nototheniids, and a decrease of crustacean prey as the season progressed. However, no seasonal changes were observed in the consumption of fish by either Imperial Cormorants or Rock Shags during this study. *Engraulis anchoita* schools approach the coast during November and December (R. Fondacaro pers. comm.), and their availability to breeding birds near their colonies may vary among years with oceanic conditions.

This study suggests that Imperial Cormorants and Rock Shags have substantial dietary

TABLE 4.   Pelagic (P) and benthic (B) fish preyed upon by Imperial Cormorants and Rock Shags at Bahía Bustamante, Argentina, during 1993 and 1994 during the four stages of the breeding cycle. Values are frequency of occurrence.

Year and species	Pre-laying		Incubation		Young chicks		Old chicks		Total	
	P	B	P	B	P	B	P	B	P	B
1993										
Imperial Cormorant	96	15	81	60	84	54	93	46	89	45
Rock Shag	61	83	80	67	85	88	76	79	75	82
1994										
Imperial Cormorant	94	52	100	67	100	76	96	42	96	53
Rock Shag	69	91	72	67	88	80	80	81	76	83

overlap, i.e., food partitioning is not demonstrated. However, ecological segregation in seabirds may be achieved through a combination of differences in diet, feeding range (both vertical and horizontal), and feeding behavior (Ashmole and Ashmole 1967, Ridoux 1994, Croxall et al. 1997). Among related species such as the Imperial Cormorant and Rock Shag, overlap in diet may be expected (Ridoux 1994), but prey size may be a more important mechanism of dietary segregation than prey type. Several studies have found differences in prey sizes between congeneric species (Ashmole and Ashmole 1967, Hulsman 1988, Fasola et al. 1989). The mean body mass of Imperial Cormorants is greater than that of Rock Shags (2.3 versus 1.5 kg; F. Quintana unpubl. data), and at Golfo San Jorge preliminary results suggest that the former feeds on larger prey (GP unpubl. data). Further studies should examine the role of prey size in the possible partitioning of food resources between the two species.

Differences in foraging range also have been found to be important in the segregation of seabird communities (Hulsman 1988, Adams and Brown 1989, Weimerskirch et al. 1988, Croxall et al. 1997). Our results on diving behavior show that Imperial Cormorant diving depth was significantly greater than that of Rock Shags, suggesting that the former species is capable of foraging on benthic prey farther away from the colonies and thus may have a wider foraging range. Recent research supports this hypotheses, as Sapoznikow and Quintana (2003) found that although both species generally foraged close to their colonies, some Imperial Cormorants traveled farther offshore during their foraging trips. Imperial Cormorants also have been observed feeding farther offshore than Rock Shags in waters around the Malvinas (Falkland) Islands (Thompson 1989, White at al. 1999).

Feeding habits also may contribute to the partitioning of food resources. Despite the similarities in the diets of Imperial Cormorants and Rock Shags, differences between the two species were found in the proportion of fish they obtained from different habitats, with Imperial Cormorants consuming a larger proportion of pelagic and demersal fish prey, particularly *Engraulis anchoita*. At Bahía Bustamante, Imperial Cormorants and Rock Shags mainly foraged individually, although the former species was observed foraging in groups on several occasions (Punta et al. 1993). Group foraging behavior was reported extensively for seabirds which prey upon dense schools of pelagic fish (Jordán 1967, Duffy 1983, Schreiber and Clapp 1987) and, consistent with this, Punta et al. (1993) reported that group foraging became more frequent at approximately the same time that *Engraulis anchoita* started to occur in diet samples. The observed differences in the proportion of pelagic and benthic prey between cormorants and shags may be the result of differences in foraging habits, with Imperial Cormorants perhaps having a wider feeding range, making greater use of the water column, and being able through group feeding to prey more effectively and in an opportunistic way upon dense schooling fish.

An overlap in diet also may reflect good feeding conditions near the colonies during the study. Substantial overlap in diet has been reported in seabird breeding assemblages (Furness and Barret 1985, Croxall et al. 1997). This would explain the relatively extensive overlap in diet (this study) and foraging areas (Sapoznikow and Quintana 2003) as a result of both species feeding relatively close to the colony on abundant food resources. At times of food scarcity, resource overlap between Imperial Cormorants and Rock Shags may be reduced through a combination of differences in diving capabilities, maximum potential foraging ranges, and foraging behavior. Information on prey abundance and availability is needed to adequately interpret patterns of resource overlap among species (Wiens 1989).

ACKNOWLEDGMENTS

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